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Cyperus blepharoleptos (Cuban bulrush) suitable habitat expansion in future climate scenarios

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ABSTRACT

Invasive species are one of the foremost threats to global biodiversity, and predicting where they can inhabit is of primary concern for researchers and resource managers. Ecological niche models (ENMs) are a useful tool for addressing this problem. This study focuses on *Cyperus blepharoleptos* (Cuban bulrush), an aquatic sedge that is invasive in the southeastern United States. To model the ecological niche of *C. blepharoleptos,* 1,137 records were compiled from North and South America and partitioned into training and testing data. Five BioClim variables (BIO1, BIO7, BIO12, BIO14, and BIO15) were selected as environmental variables for modeling. Conservative and speculative ENMs were constructed for *C. blepharoleptos* using maximum entropy (Maxent). The ENMs were then used to predict habitat suitability, recent climate, and best-case future climate (high greenhouse gas mitigation) for 2040, and worst-case future climate for 2040 (low mitigation). Recent climate predictions suggest suitable habitat in the Southeast in areas currently uninvaded, namely Georgia, South Carolina, North Carolina, Arkansas, and eastern Texas. Under future climate scenarios, suitable habitat is predicted to expand into Tennessee, Oklahoma, and Virginia. Ultimately, future climate scenarios predict between a 110% and 160% increase in niche area over recent climate predictions. These predictions are compared to previous studies and future research directions are discussed.

Key words: climate change, Cyperaceae, ecological niche model, invasive species, Maxent, *Oxycaryum cubense*

INTRODUCTION

In the field of invasion ecology, one of the most important research questions asks where an invasive species could be found on the landscape, and researchers often answer this question with ecological niche models (ENMs; Peterson 2001). Correlative niche models are a popular approach, because they generally provide more model complexity per unit effort than their mechanistic counterparts (Peterson et al. 2015). For example, mechanistic niche models require (often time and labor intensive) physiological experiments to describe aspects of an ecological niche, whereas correlative approaches can leverage publicly available species records and environmental data to generate models, requiring less effort. One major challenge with using correlative niche models for invasive species ENMs is that most correlative approaches assume that the subject species is in equilibrium with its environment; this assumption is often egregiously violated by invasive species as they experience periods of range expansion following introduction (Elith et al. 2010, Pili et al. 2020). Additionally, as the global climate changes, climatic conditions are predicted to shift, further positioning species out of equilibrium (Elith et al. 2010, Peterson et al. 2018). However, Maxent (abbreviation of "maximum entropy") is a newer, publicly accessible approach that is robust to violations of this assumption and can use large, publicly available, presence-only data sets (Phillips et al. 2006, Elith et al. 2010). These strengths make Maxent a popular approach for generating ENMs of invasive species (Lázaro-Lobo et al. 2020, Gebhart and Wersal 2023, Sánchez-Restrepo et al. 2023). This approach was used to generate an ENM for *Cyperus blepharoleptos* Steud. (Cyperaceae; Cuban bulrush; syn: *Oxycaryum cubense, Scirpus cubensis*), an aquatic plant that is invasive in the southeastern United States.

Cyperus blepharoleptos is distributed throughout tropical and subtropical Africa and America; in the United States, it is an emerging, invasive species, which is rapidly expanding its distribution in the Southeast (Bryson et al. 2008, Larridon et al. 2011, Schmid and Turnage 2023). This sedge is invasive in the United States and presumed native in Africa and Latin America (Lye 1971, Bryson et al. 1996, 2008). Once introduced to an ecosystem, *C. blepharoleptos* often develops dense mats (tussocks) of plant material amongst the emergent vegetation and tends to grow on top of other vegetation; it is because of this habit that *C. blepharoleptos* is often described as epiphytic (Watson and Madsen 2014, Clarke et al. 2023, Squires et al. 2024a). These tussocks can be rooted on vegetation or in the sediment, or they can fragment, with sections becoming free-floating (Bryson et al. 2008, Clarke et al. 2023). Populations of *C. blepharoleptos* can be large and dense, impeding navigation, displacing native species, and altering the structure of the invaded ecosystem (Bryson and Carter 2008).

In the United States, *C. blepharoleptos* was likely introduced in the late 19th century, with the first records in herbaria collected from Alabama and Louisiana in 1878 (McNeal UNA00001491; Mohr GH 02503413; Mohr GH 02503414; Squires et al. 2024b). Until recently, *C. blepharoleptos* in the United States was reported as sporadic in Florida and Louisiana, with very limited ranges in Mississippi, Alabama, Georgia, and Texas (Bryson et al. 2008,

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Watson and Madsen 2014). Currently, the plant is quite common in Florida and Louisiana, and expanding its range in Mississippi and Alabama (GBIF.org 2024). Because of its recent range expansion, a recent study modeled the effect of temperature on *C. blepharoleptos* growth (Squires et al. 2024a). These mechanistic models suggest that *C. blepharoleptos* can expand its range far past its current extent; however, models from Squires et al. (2024a) are solely based on temperature; many other environmental factors that were not assessed in this study (water and nutrient availability, biotic interactions, etc.) influence the ecological niche of an organism (Peterson 2001, Squires et al. 2024a). At present, no ENMs for *C. blepharoleptos* account for both temperature and precipitation in their construction. Including precipitation in these models is important because precipitation regime can affect availability of water, and therefore *C. blepharoleptos* habitat (Viana 2017). The objectives of this study were 1) to use a correlative niche modeling approach (Maxent) to model the ecological niche of *C. blepharoleptos* based on temperature and precipitation levels and 2) to predict the geographic distribution of its suitable habitat in recent and future climate scenarios. We hypothesized that, because the range of *C. blepharoleptos* is currently expanding (Bryson et al. 2008, Watson and Madsen 2014), its ENM will predict suitable habitat beyond its current, known distribution.

MATERIALS AND METHODS

Data acquisition

The environmental variables used to train the niche model were bioclimatic (BioClim) variables that were selected *a priori* because of their biological significance and because they are not highly multicollinear ($\rho \leq 0.80$). Five BioClim variables were ultimately selected: BIO1 (annual mean temperature), BIO7 (annual temperature range), BIO12 (annual precipitation), BIO14 (precipitation of driest month), and BIO15 (precipitation seasonality). Rasters for these BioClim variables were obtained at the 30–arc second resolution (pixels roughly 1 km^2) from the WorldClim climate data consortium (Fick and Hijmans 2017). Notably, extreme temperatures (e.g., temperature maximum temp of the hottest month) were not included as environmental variables because of their high degree of collinearity with BIO1. However, these extremes are partially accounted for in BIO7. BioClim variables were generated from global climate data for the temporal range of 1970–2000, and were considered representative of recent climate for the purposes of this study (Fick and Hijmans 2017).

An occurrence data set for *C. blepharoleptos* was compiled from a list of presence-only data that were obtained from a Global Biodiversity Information Facility (GBIF) query resulting in 6,434 records (GBIF.org 2024). In addition to GBIF data, three verifiable occurrences were added to data set (Schmid 388 MISSA040153; Horton 417 MISSA040149; Horton pers. comm.). To remove redundant records and reduce sampling bias, the data set was thinned to one record per 1 km^2 using the "spThin" R package (Aiello-Lammens et al. 2019). After thinning, the data set consisted of 1,137 records. This data set included only data from the Americas; although *C. blepharoleptos* occurs in Africa, available reports of *C. blepharoleptos* across the African continent are sporadic and uneven. Therefore, we considered data from Africa poorly suited for this application. The data set was then separated at random into a training data set and testing data set. The training data set contained approximately 60% ($n = 683$) of the thinned records whereas the testing data set contained approximately 40% ($n = 454$).

Ecological niche modeling

The R packages "ENMeval" (Kass et al. 2023) and "dismo" (Hijmans et al. 2023) were primarily used to generate ENMs and model predictions in RStudio.[1] Both ENMeval and dismo can run Maxent[2] in tandem with RStudio to generate Maxent ENMs (Phillips et al. 2020). The training data set of *C. blepharoleptos* records was used to train ENMs with the records from the testing data set being completely withheld from training. Ecological niche models were trained using the five selected BioClim (BIO1, BIO7, BIO12, BIO14, and BIO15) variables from the recent climate scenario as predictors. A set of 2,000 randomly placed background (pseudo-absence) points were used to train the models. The modeling was conducted in two different iterations that we termed "conservative" and "speculative." These iterations differed in their regularization multipliers (RM), which penalizes model complexity more as RM increases. The conservative iteration had models with lower RMs (*ergo* more complex models), whereas the speculative iteration had models with greater RMs. The conservative iteration was considered conservative because the more complex models with lower RMs tend to constrain the ecological niche to match the extent of the training data more closely (Phillips et al. 2006, 2017). Likewise, the speculative models are simpler and tend to predict more niche space beyond the extent of the training data (Phillips et al. 2006, 2017).

Both model iterations were tuned using four feature classes (FCs; linear, linear–quadratic, linear–quadratic–hinge, and hinge) and two RMs (1 and 2 or 3 and 4); these combinations of FCs and RMs generated eight different candidate models per iteration, which were subjected to model selection. First, candidate models with an omission rate (OR) $>$ 0.05 were excluded from model selection. In this context OR refers to the proportion of occurrences not included in model training. Second, the model with the lowest corrected Akaike information criterion (AICc) was considered the best-fit model. The AICc represents the logarithmic relationship between likelihood function and the maximum likelihood estimate added to the number of estimated parameters (Portet 2020). Finally, in instances where there is substantial support for multiple best-fit models (i.e., ΔAICc: $|x| \leq 2$), the most parsimonious model was considered as the best-fit model (Burnham and Anderson 2002). The predictive power of the best-fit model was determined using the receiver operator curve area under the curve (AUC) and the continuous Boyce index (CBI; Hirzel et al. 2006, Elith et al. 2011). Both of these metrics compare the predictive power of the best-fit model to a null model that assumes the distribution of *C. blepharoleptos* was unaffected by the environmental predictors. The AUC values range from 0 to 1, with the null model equaling 0.5, whereas the CBI ranges from -1 to 1 with the null model equaling 0 (Hirzel et al. 2006).

Table 1. The percent change in habitat area (Δ area) for conservative and speculative model predictions in future climate scenarios. The Δ area represents change compared to recent climate scenario.

Scenario[1]	Iteration	Δ area (%)			
		Poor	Moderate	High	Total
SSP1	Conservative	86.7	234.2	568.6	151.2
	Speculative	58.6	256.7	410.2	118.0
SSP5	Conservative	79.9	232.8	750.4	156.2
	Speculative	50.0	272.3	535.3	120.6

[1]Scenario descriptions: SSP1 = best-case climate scenario for 2040; SSP5 = worst-case climate scenario for 2040.

Following model selection, best-fit models for both iterations were used to predict geographic habitat suitability in the form of probability of inhabitance (*P*), across the North and South American continent in a raster at the 30–arc second resolution. Suitable habitat values were scaled using the "cloglog" function native to Maxent (Phillips et al. 2020). The suitable habitat predictions were calculated in a recent climate scenario and two future climate scenarios: best case and worst case by 2040. The best-case scenario was shared socioeconomic pathway (SSP) 1-2.6 and the worst-case scenario was SSP5-8.5. These SSPs represent scenarios based on different global responses to climate change and greenhouse gas emission. Socioeconomic pathway 1 represents a scenario with low challenges to climate change mitigation, whereas SSP5 predicts high challenges to mitigation (Riahi et al. 2017). Future climate scenarios consisted of BioClim data as predicted by the HadGEM 3 climate model family, which was prepared for the Coupled Model Intercomparison Project Phase 6 (Roberts 2017). Future climate scenario data were obtained as raster files from the WorldClim consortium at the 30–arc second resolution (Fick and Hijmans 2017). Potential habitat was categorized into four classes: unsuitable ($P \leq 0.25$), poorly suitable ($0.25 < P \leq 0.50$), moderately suitable ($0.50 < P \leq 0.75$), and highly suitable ($P \leq 0.75$). All data processing and modeling was conducted in R[3] and RStudio, and all mapping was conducted in ArcGIS Pro.[4] All data and code used in the preparation of this paper were submitted to the Mississippi State University institutional repository and are publicly available† (https://doi.org/10.54718/VZHV3738).

RESULTS AND DISCUSSION

Of the six candidate models constructed for both modeling iterations of this study, none had an OR > 0.05, so all were included in model selection for both iterations. The model with the lowest AICc was selected as the best-fit model for both iterations; the best-fit model had a significantly lower AICc than all other candidate models in both iterations. The conservative best-fit model had an RM of 1 and an FC that included linear, quadratic, and hinge functions. The total number of coefficients in the conservative best-fit model was 88. The speculative best-fit model had an RM of 3 and an FC that included linear, quadratic, and hinge functions. The total number of coefficients in the speculative best-fit model was 34. In the context of Maxent ENMs, these coefficients are mathematical constraints imposed on the model so the predictions more closely resemble the training data (Elith et al. 2011). It was expected that the conservative model would have a greater number of coefficients than the speculative model. Both the conservative best-fit model (AUC = 0.874; CBI = 0.998) and the speculative best-fit model (AUC = 0.853; CBI = 0.988) were highly predictive compared to the null model. The difference between training and validation AUC was low for both the conservative best-fit model (ΔAUC = 0.037) and speculative best-fit model (ΔAUC = 0.031), indicating a low degree of overfitting. For the conservative best-fit model, percent contribution of BioClim variables were: BIO1 = 23.4%, BIO7 = 34.8%, BIO12 = 13.3%, BIO14 = 22.8%, and BIO15 = 5.6%. For the speculative best-fit model, percent contribution of BioClim variables were BIO1 = 22.2%, BIO7 = 39.8%, BIO12 = 12.2%, BIO14 = 23.5%, and BIO15 = 2.3%.

Generally, under all three climate scenarios, the speculative best-fit model predicted more *C. blepharoleptos* suitable habitat than the conservative best-fit model (Table 1). The difference in niche area (millions of pixels) between the speculative model predictions and conservative model predictions were 4.816, 1.402, and 1.237 for the recent, SSP1, and SSP5 climate scenarios, respectively. The difference in area between the conservative and speculative best-fit model is greatest in the recent climate and lower in both SSP1-2.6 and SSP5-8.5 (Table 1). From recent climate to SSP1-2.6 to SSP5-8.5, both the conservative and speculative best-fit models predict increasing suitable habitat for *C. blepharoleptos* (Table 1). Additionally, from recent climate to SSP1-2.6 to SSP5-8.5, both the conservative and speculative best-fit models predict decreasing poorly suitable habitat and increasing moderately and highly suitable habitat (Table 1).

The predictions from our *C. blepharoleptos* ENMs support our hypothesis that *C. blepharoleptos* is predicted to expand its range beyond its current distribution, according to its ecological niche. Based on these ENMs, the ecological niche of *C. blepharoleptos* is predicted to expand, in both North and South America, under future climate scenarios (Figures 1–3). Specifically, large portions of Georgia, South Carolina, North Carolina, Arkansas, and eastern Texas are predicted to have suitable habitat for *C. blepharoleptos* well beyond its current described range. Under future climate scenarios, these uninvaded areas of suitable habitat are predicted to expand into other nearby states like Tennessee, Oklahoma, and Virginia (Figures 2 and 3). The greatest gains in niche area are predicted to occur under more extreme climate change (i.e., SSP5-8.5; Figures 1–3). These results are consistent with the general consensus on *C. blepharoleptos* as an emerging invasive species that is currently expanding its invaded range. Prior publications account noteworthy records of *C. blepharoleptos* expanding its range in the southeastern United States and this trend appears to be ongoing (Bryson et al. 1996, 2008). The high contributions of BIO1 and BIO7 to the best-fit models suggest that changing temperature is the primary driver of *C. blepharoleptos* niche

†Disclaimer: Files are available as a large .zip file (6.1 Gb) on repository posting. Download and decompression duration may be long and will depend on network and workstation performance.

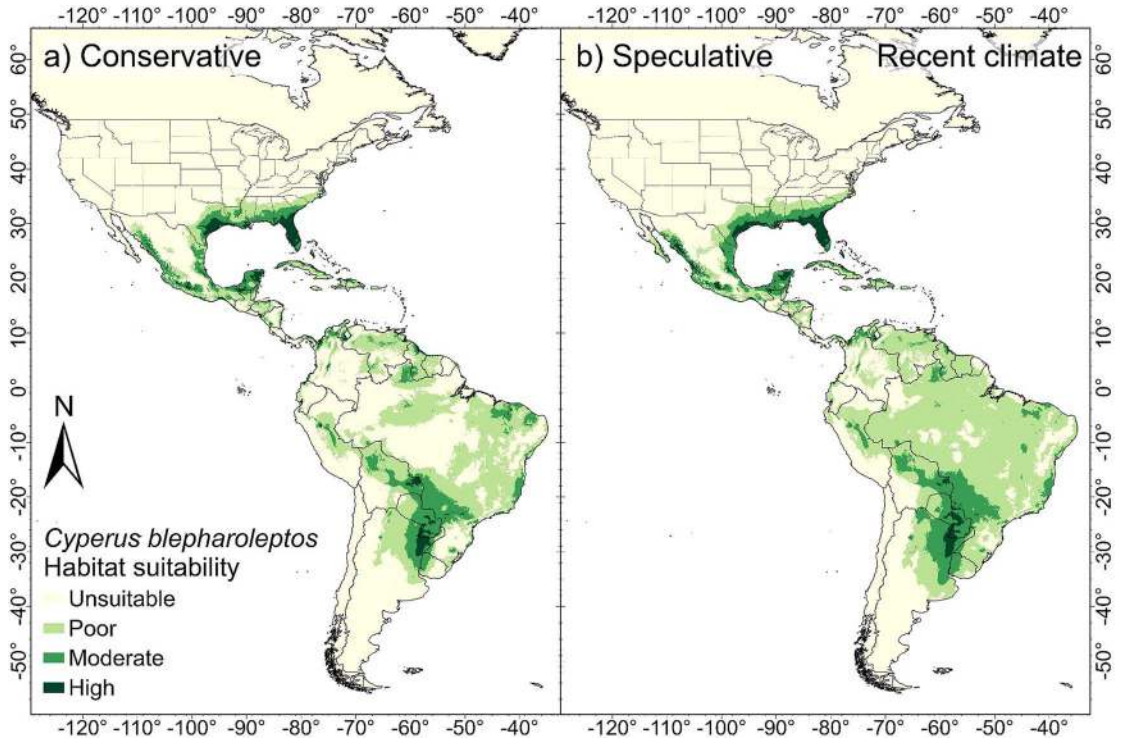

Figure 1. Maps of predicted *C. blepharoleptos* habitat suitability under the recent climate scenario for (a) the conservative best-fit model and (b) the speculative best-fit model.

expansion. Under the recent climate scenario, suitable habitat for *C. blepharoleptos* extends northward to only about 37°N whereas under the most extreme scenario (SSP5-8.5) the extent of suitable habitat is expected to extend as far north as 39°N, with some small disjunctions of suitable habitat in the Great Lakes region of the United States and Canada from the speculative prediction (Figures 1 and 3). Additionally, under future scenarios, the currently suitable

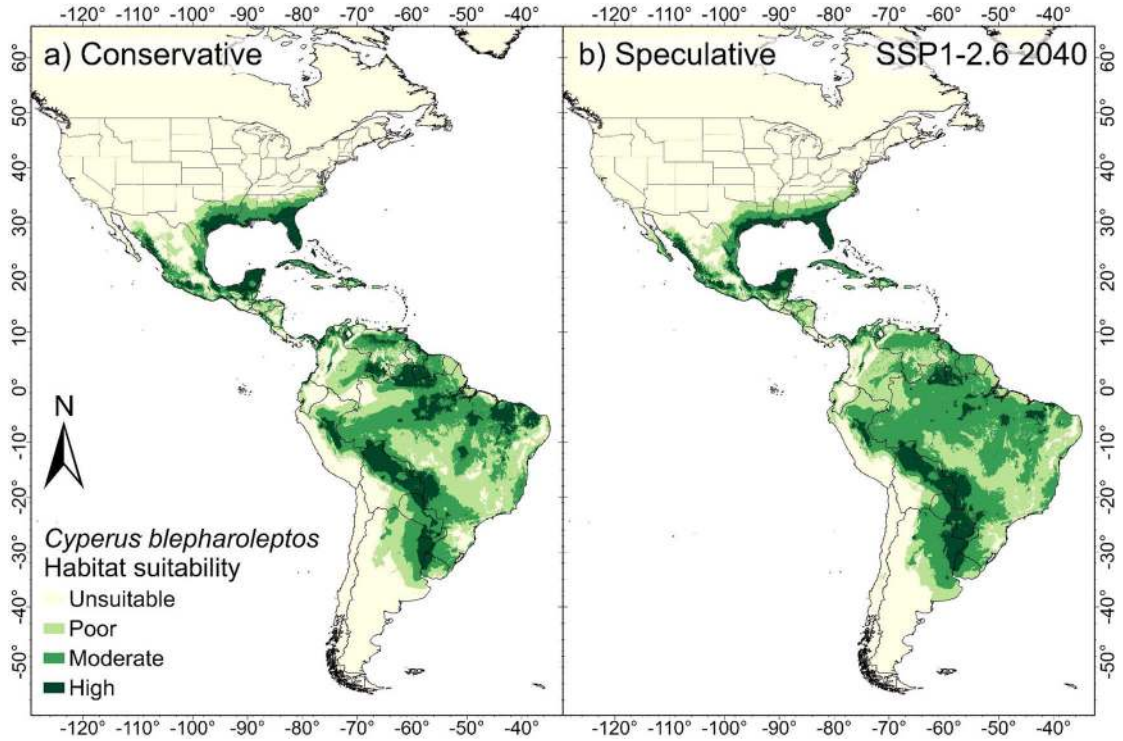

Figure 2. Maps of predicted *C. blepharoleptos* habitat suitability under the shared socioeconomic pathway (SSP) SSP1-2.6 climate scenario at year 2040 for (a) the conservative best-fit model and (b) the speculative best-fit model.

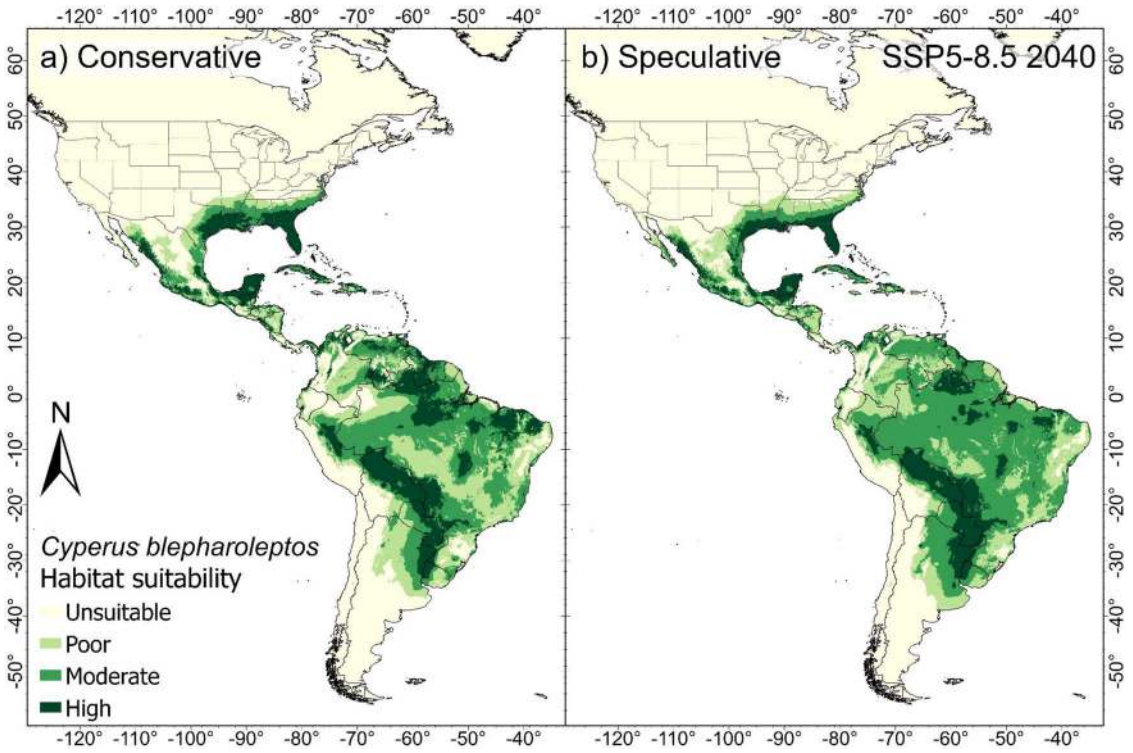

Figure 3. Maps of predicted *C. blepharoleptos* habitat suitability under the shared socioeconomic pathway (SSP) SSP5-8.5 climate scenario at year 2040 for (a) the conservative best-fit model and (b) the speculative best-fit model.

habitat is expected to increase in quality throughout much of its current invaded range, potentially exacerbating the severity of current invasions (Figures 1–3).

Previous research has modeled the effects of climate on the ecological niche of *C. blepharoleptos,* specifically how accumulated degree days affect biomass in the southeastern United States (Squires et al. 2024a). The models from Squires et al. (2024a) predicted between 6,400 and 8,000 ADD were needed for the tested *C. blepharoleptos* populations to reach peak biomass. Their models also found that the base temperature threshold for growth was between −6 C and −2 C for tested populations (Squires et al. 2024a). Squires et al. (2024a) suppose that solely based on the critical values from their models, that *C. blepharoleptos* could inhabit north of 40 N. Our models predict that suitable habitat this far north is unlikely under any scenario in the next 15 yr (with the exception of the speculative predictions in the worst-case scenario); however, this inconsistency does not necessarily dissent the findings of Squires et al. (2024a), but rather demonstrates key differences between the methods. The predictions in Squires et al. (2024a) are solely based on ADD and base temperature threshold and therefore only describe a portion of the fundamental niche of *C. blepharoleptos.* The fundamental niche of an organism is complex and multidimensional, and estimating the fundamental niche via mechanistic approaches requires complex models with multiple indices for an accurate estimation (Peterson et al. 2015, Angilletta et al. 2019). By contrast, correlative approaches (like Maxent) make it easier to estimate more dimensions of the ecological niche, but they are not based on empirical experiments (Peterson et al. 2015). Without describing the mechanisms that determine the fundamental niche, correlative approaches predict an intermediate between the fundamental and realized niche (Lobo et al. 2010, Peterson et al. 2015). There are several possible reasons that explain why there is a discrepancy between our findings and the findings of Squires et al. (2024a) such as uneven distribution of occurrence data and an expanding invaded range. Although there are inconsistencies between the findings of this study and Squires et al. (2024a), both agree that *C. blepharoleptos* is not in a state of equilibrium and the range expansion of this species should be thoroughly monitored. Although our models did not specifically measure biological mechanisms that govern the ecological niche of *C. blepharoleptos*, BIO1 and BIO7 had the greatest contribution to both of our ENMs. Both variables are measures of temperature, suggesting that temperature is more influential on the ecological niche of *C. blepharoleptos* than precipitation. We suspect that the predicted increase in mean annual temperature is a major driver of the expansion of the predicted *C. blepharoleptos* niche, as the HadGEM3-GC31-LL models predict warmer average annual temperatures further north (Roberts 2017). In actuality, an increase in the annual growing degree days (GDD) would likely be the mechanism for an expanded *C. blepharoleptos* niche in future climates as an analysis of climate change over the 20th century has shown an increase in annual GDD (Kukal and Irmak 2018). The lower importance of precipitation explains why wetland ecosystems are widely and densely distributed throughout the Americas, even in regions that experience less precipitation (Hu et al. 2017).

With regards to correlative niche modeling approaches, it is important to consider multiple scenarios when predicting ecological niches. Making predictions based on only a single model or scenario can cause stakeholders to rely on assumptions about the study system that may be erroneous. Although there are no standard protocols to "properly" tune Maxent ENMs, the Maxent approach is thoroughly tested and discussed in the literature (Phillips et al. 2006, Elith et al. 2010, Fernández and Hamilton 2015). Broadly, the literature on the ecology of *C. blepharoleptos* is depauperate, and this field of *C. blepharoleptos* ecology needs to be more thoroughly developed.

Another frequently discussed aspect of *C. blepharoleptos* biology is the two seemingly discrete forms it can exhibit: the capitate form (AKA: monocephalous; *Oxycaryum cubense* f. *cubense*) and the anthelate form (AKA: polycephalous; *O. cubense* f. *paraguayense*; Bryson and Carter 2008, Squires et al. 2024b). These *formae* are not thoroughly described, and the evolutionary significance of these *formae* is currently unknown, however, they appear to have geographic differences with capitate populations more common in northern latitudes than anthelate populations (Bryson et al. 2008, Squires et al. 2024a). Developing separate niche models for the different *formae* could help determine whether the geographic differences are significant. Such a study would likely benefit from a niche modeling approach that uses absence data to define the boundaries between the two *formae* more precisely. Previous studies on intraspecific niche modeling have provided meaningful conclusions on within-species niche differences, assuming there are enough occurrences for strong ENMs (Maguire et al. 2018, Collart et al. 2021).

Based on our findings, we recommend Arkansas resource managers closely monitor the status of *C. blepharoleptos* in the state's waters, especially with the recent incursions documented in herbarium collections (Schmid 388 MISSA040153; Horton 417 MISSA040149). Additionally, we recommend Oklahoma, Tennessee, and North Carolina resource managers monitor their states' waters for potential incursions of *C. blepharoleptos*.

SOURCES OF MATERIALS

[1]RStudio (version 26.2.4); Posit Software, Boston, MA.
[2]Maxent (version 3.4.3); American Museum of Natural History, New York, NY.
[3]R (version 4.3.2); R Foundation, Vienna, Austria.
[4]ArcGIS Pro (version 3.1.0); Esri, Redlands, CA.

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